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Morphologic and Reproductive Biology of Two Species of the Buccinid Gastropod Genus *Aeneator* Finlay, 1927 from Southern Chilean Fjords

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Abstract. The present study describes new records for the buccinid gastropods *Aeneator fontainei* (D'Orbigny, 1841) and *Aeneator loisae* Redher, 1971 collected in Chile's southern fjord region in 2001 and 2002. This report now extends the distribution of these species to 46°S. Observations on the morphologies of their egg capsules showed intraspecific differences in form, presence of indentations on the borders and location of the pore. Differences were also noted between the juveniles' shell apertures of the two species; in *A. fontainei* the border is smooth and sharpened, while in *A. loisae* it is undulant due to the presence of exterior ribs. One intracapsular specimen of *A. fontainei* shows the presence of a penetration on the last shell whorl. This perforation exhibited marked denticulations when viewed in the scanning electron microscope, suggesting the occurrence of intracapsular cannibalism by the juvenile snails. It was concluded that these species have direct holobenthic development.

INTRODUCTION

The present study presents new data on neogastropod molluscs of the family Buccinidae. This family has representatives in most of the world's oceans, from the poles to the equator, and inhabits a wide variety of mainly marine environments (Hayashi, 2005). It is one of the most diverse and abundant families of caenogastropods represented by 120 genera with at least 1000 species in the world (Vaught, 1989; Kantor, 2003). There are 14 genera present on the Pacific coast of north and South America from Baja California to Perú and northern Chile (Keen, 1971). McLean and Andrade (1982), revised the taxonomy of the genus *Aeneator* whose species are known from New Zealand and Chile. The buccinids of the present study include *Aeneator fontainei* (D'Orbigny, 1841), the most common Chilean species of the group, and *Aeneator loisae* Redher, 1971. This last species was included in subgenus *Ellicea* Finlay, 1927, which was reduced to synonymy by Powell (1979) (*fide* McLean & Andrade, 1982).

A. fontainei has been reported from Bahia Independencia, Perú (14°13′S) to Punta Toro, Chile (33°01′S) and *A. loisae* from Coquimbo (29°58′S) to Cabo Carranza (35°27′S), Chile (McLean & Andrade, 1982).

At present, reproductive aspects such as the pattern of oviposition, morphology of capsules (Gulbin, 2000; Martell et al., 2002), larval protoconch and soft parts such as stomach characters (Kantor, 2003) and penis morphology (Harasewych & Kantor, 2002) are specific characteristics of important taxonomic value, especially among the neo and mesogastropods. Knowledge of the reproductive aspects of Chilean gastropods is limited to a few subtidal species from the northern Chilean coast. One of the best studied of the muricids is *Chorus giganteus* Lesson, 1830, which inhabits subtidal soft-bottom muddy sands and deposits its egg capsules on shells of congeners, in which larval stages develop through to eclosion and release of benthic-feeding juvenile snails (Gallardo, 1980).

Biological data on *A. fontainei* and *A. loisae* are scarce and primarily restricted to morphological characteristics of their shells (D'Orbigny, 1841; McLean & Andrade, 1982; Ramirez, 1990; Guzman et al., 1998); some population data also exists (Alarcon et al., 1999). The objective of the present study is reporting the occurrence of these two species in Chile's fjord region, thus extending their known geographic range by 10° in latitude. An attempt has also been made to add to the knowledge of their adult morphology and to present new data on their egg capsules and the morphology of intracapsular juveniles.

MATERIALS AND METHODS

Data and biological material were collected during Cimar Bio-oceanographic cruises 7 and 8 (Osorio et al., 2005; Osorio et al., 2006) which formed part of the "Biodiversity of Austral Fjords" projects sponsored by the Chilean Naval Oceanographic Committee (Comité Oceanográfico Nacional de Chile). The cruises visited inshore waters between 43°45′S and 46°05′S on July 2001 and 2002. Samples containing molluscs were fixed in 10% formalin-seawater, and later stored in 70% alcohol for subsequent identification. Adult specimens of *A. fontainei* and *A. loisae* were photographed and

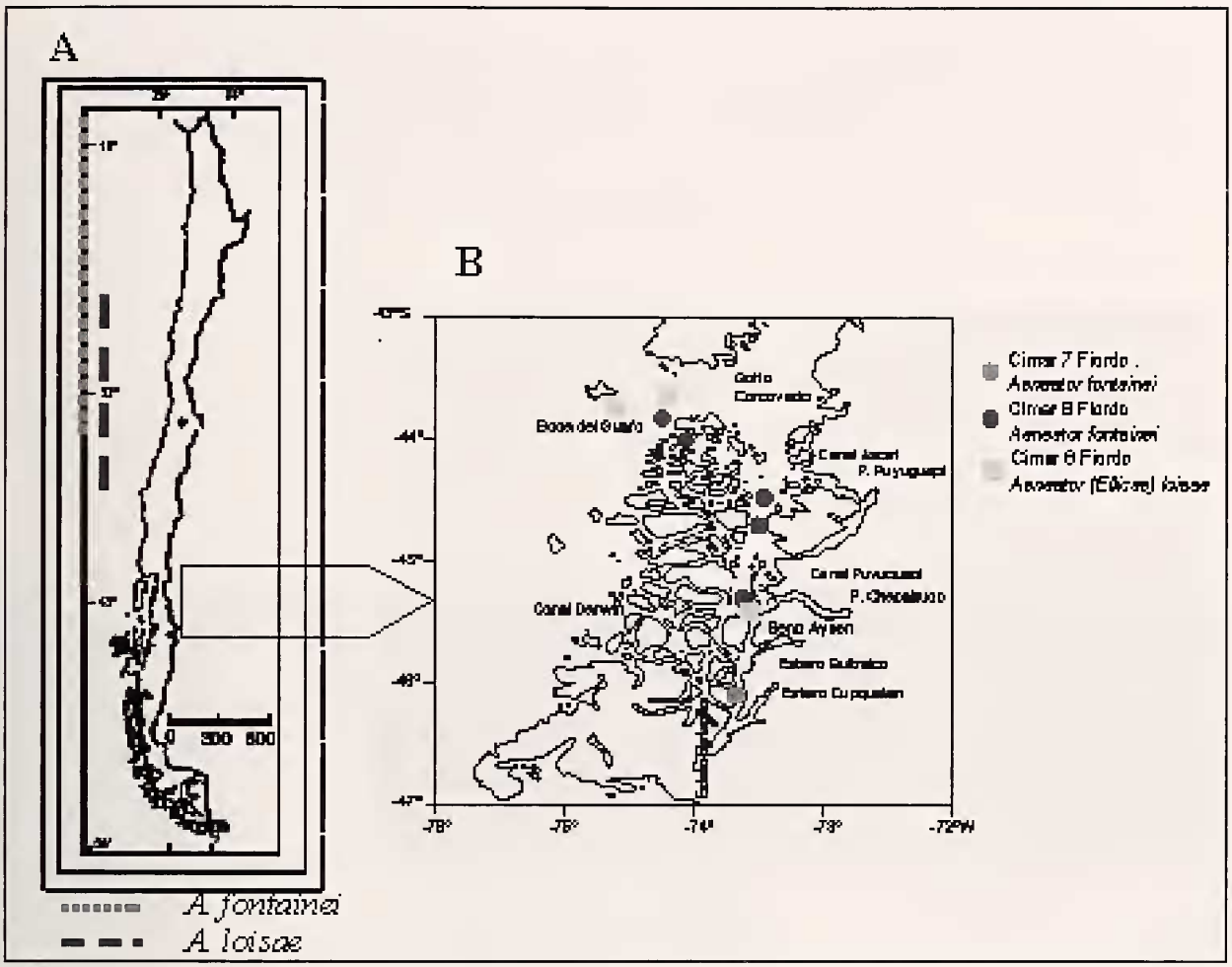


Figure 1. **A.** Original geographic distribution of *A. fontainei* and *A. loisae* and location of the Chilean austral fjord region. **B.** Amplification of the distribution of *A. fontainei* and *A. loisae* as a result of collections made during CIMAR fjord cruises 7 & 8.

measured with vernier calipers. Shell length is the maximum dimension parallel to the axis of coiling, shell width the maximum dimension perpendicular to length. The morphology of the egg capsules of these snails was described using drawings made with a camera lucida attached to a Leitz stereo microscope. A total of 32 capsules from *A. fontainei* and one capsule from *A. loisae* were opened centrally to obtain the contained larvae for morphological observation. Later, the egg capsules and juveniles of both species were measured with a camera lucida and scale, to 0.01 mm, using an ocular micrometer in the stereo microscope and also photographed using a dark field in conjunction with both reflected and transmitted light. The juveniles were also observed and photographed using a Zeiss DS M 940 scanning electron microscope (SEM). The location of voucher specimens is Museo Nacional de Historia Natural (Chile), collection numbers: 5687 to 5696.

RESULTS

Six individuals of *A. fontainei* were obtained, of which two were adults, and four *A. loisae* of which three were adults. These findings represented a new record for the presence of these species in this region, with *A. fontainei* at more than 13° and *A. loisae* at more than 10° farther south than previously recorded (Figures 1A, B). Geographic locations and oceanographic data for each individual of the two species collected are listed in Table 1.

Shell Measurements

The sizes of the shells of the adult specimens of *A. fontainei* ranged from 10.3 to 12.8 cm, while those of *A. loisae* were from 10.5 to 12.8 cm in total length (Figures 2A, B). Table 2 presents the details of the

Table 1

Number of specimens observed with corresponding oceanographic data for *A. fontainei* and *A. loisae* obtained during CIMAR Fjord cruises 7 and 8.

Species	Number of specimens	Locality	Date	Latitude (south)	Depth (m)	Temperature (°C)	Salinity (‰)
			Cruise CIMAR Fjord 7				
A. fontainei	1	Estero Elefantes	07/2001	46°05,01′	60	9.3	28.09
			Cruise CIMAR Fjord 8				
A. fontainei	1	Canal Moraleda	07/07/2002	44°25,30′	200	*	*
	1	Canal Moraleda	07/07/2002	44°40,80′	345	10.1	33.52
	1	Canal Moraleda	07/07/2002	45°21,20′	75	9.7	31.25
	1	Canal Tuamapu	20/07/2002	44°00,00′	220	9.9	33.31
	1	Canal Tuamapu	20/07/2002	43°58,50′	160	9.9	33.45
A. loisae	1	Boca del Guafo	06/07/2002	43°45,20′	230	9.6	34.04
	2	Boca del Guafo	06/07/2002	43°41,00′	200	9.8	33.94
	1	Canal Moraleda	07/07/2002	45°21,20′	75	10.1	33.51

* No information

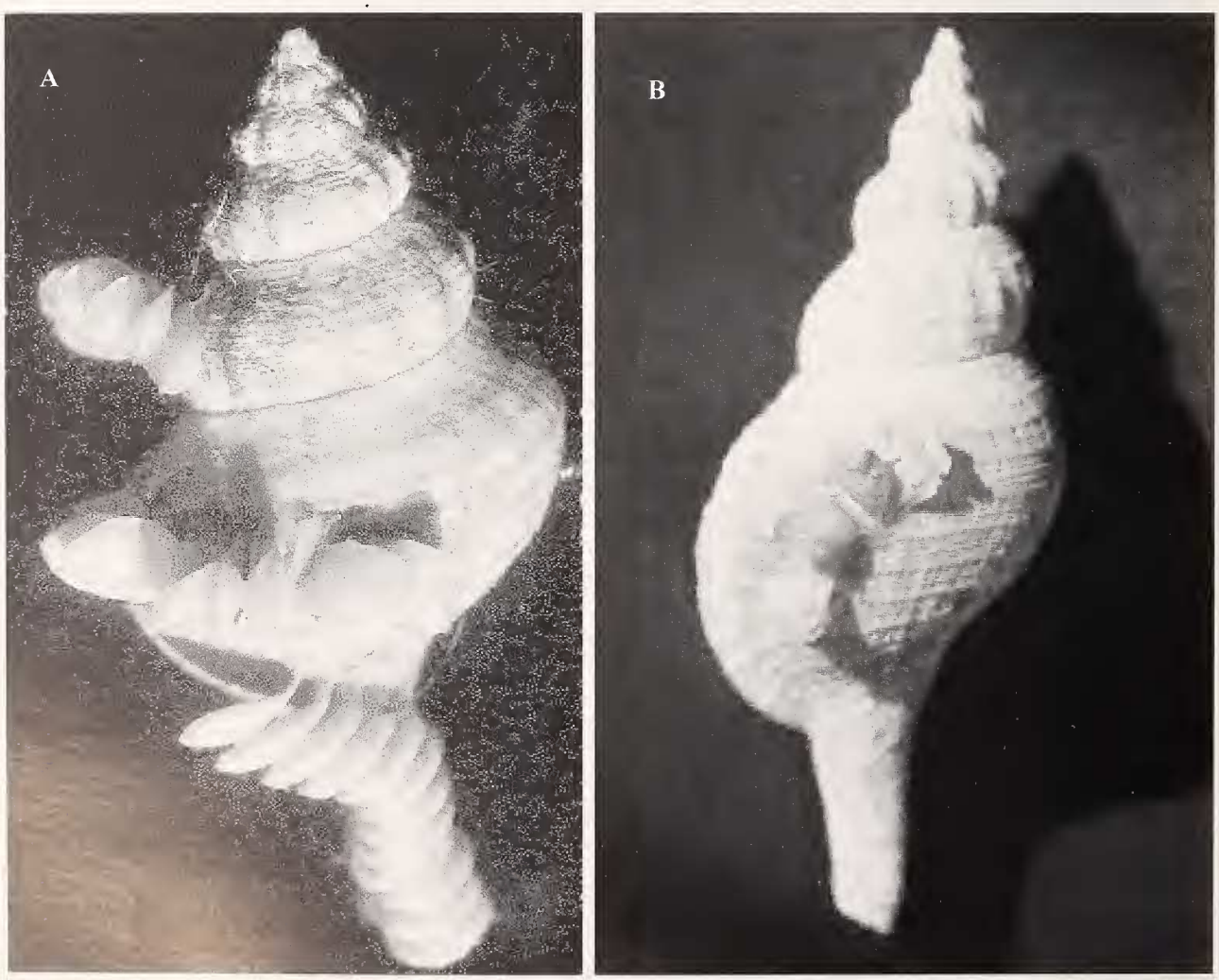


Figure 2. **A.** *A. fontainei* with three rows of egg capsules deposited on its shell. **B.** *A. loisae* with egg capsules deposited on its shell.

Table 2

Size, sex, and observations on *A. fontainei* and *A. loisae* from Table 1.

Species	Length (cm)	Width (cm)	Sex	Observations
		Cruise CIMAR Fjord 7		
A. fontainei	10.3	4.5	F	Alive with egg capsules
		Cruise CIMAR Fjord 8		
A. fontainei	2.4	1.0	—	No presence of soft parts
	3.9	2.0	—	No presence of soft parts
	12.8	5.5	M	Alive
A loisae	10.5	5.0	M	Alive with egg capsules
	12.8	6.3	M	Alive with egg capsules
	11.9	5.7	—	No presence of soft parts
	2.2	1.0	—	No presence of soft parts

F: Female; M: Male.

measurements, sex and individual observations made on each specimen; sexually indeterminate specimens were those with empty shells. Two individuals of *A. fontainei* and two *A. loisae* were found in the broken state, lacking soft parts.

Descriptions of Egg Capsules

A female specimen of *A. fontainei* collected in July 2001 was found with 32 egg capsules deposited on its shell, arranged in three rows (Figure 2A). The first row of (12) egg capsules was arranged antero-dorsally on the dorsum of the siphonal canal. The second row of (11) capsules occurred on the dorsum of the last shell whorl, as did the third row of (9) capsules. Each egg capsule was sub-circular (mean length 9.75 mm; mean width 8.89 mm; n = 32), biconvex, yellowish in color and opaque. All the capsules had a short peduncle with a very narrow elongated basal portion which was attached to the surface of the shell. Each capsule had a pore on its apical extreme, in a lateral sub terminal position.

The material filling the pore breaks up and dissolves in stages prior to eclosion. The diameter of the pore varied between 0.80 and 2.4 mm (mean 1.57 mm; n = 29). Two indentations were notable on the lateral borders of each capsule, which differed in depth and location among the capsules (Figures 11A, B). Numerous capsules contained juvenile snails within a transparent liquid containing tissue remains. A few capsules were stronger and thicker than others, and contained larger amounts of tissue remains and healthy eggs, but no juvenile specimens.

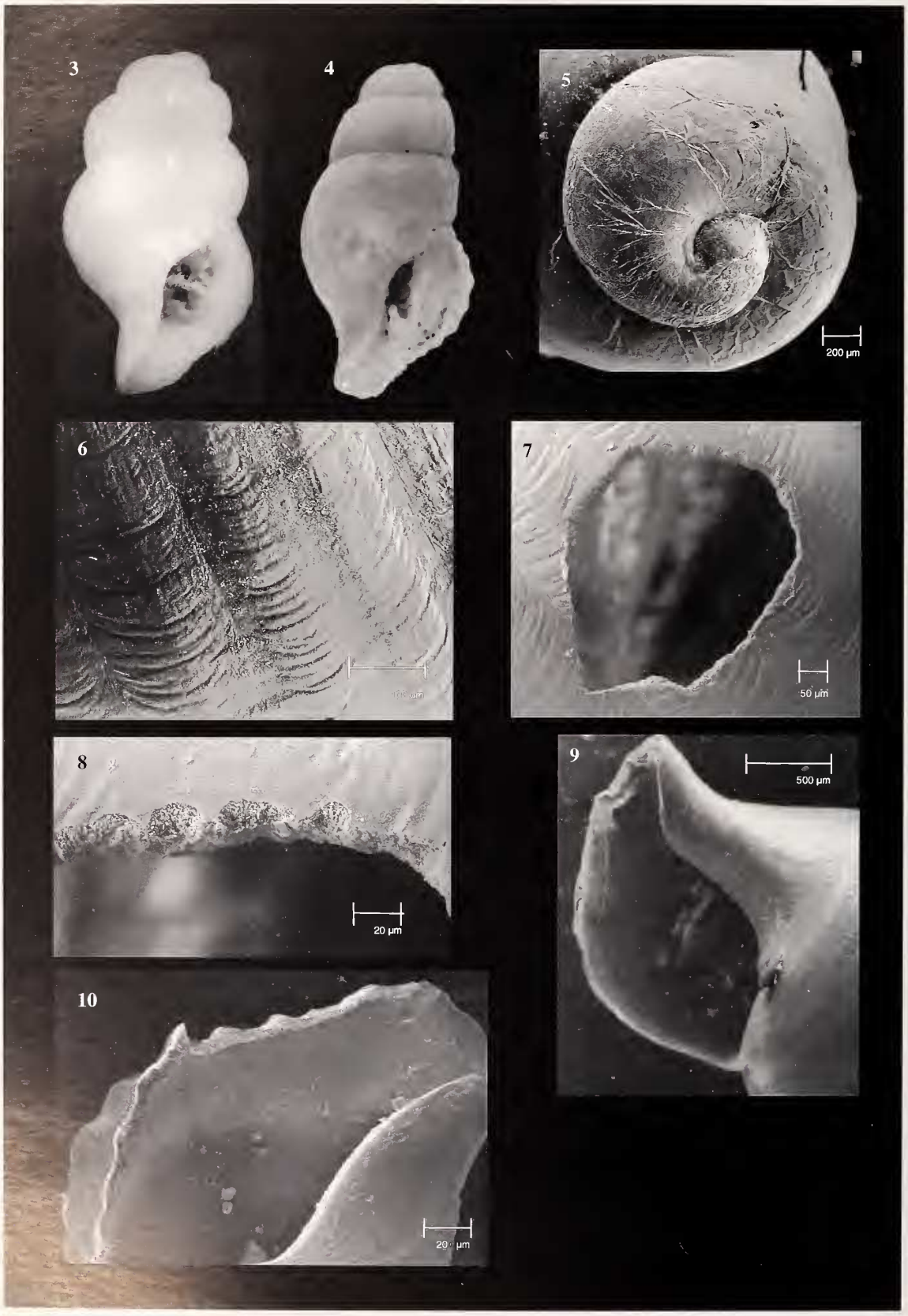
Of the *A. loisae* specimens which carried egg capsules, one had a row of 12 capsules (Figure 2B) of which eight were completely or partially broken. The other *A. loisae* specimen had a row with two partially broken, hatched capsules and the remains of ten peduncles along the length of the shell. The latter egg capsules could be differentiated from those of *A. fontainei* by their subcircular oblique form (mean length 8.90 mm; mean width 7.90 mm, n = 7), and by the location of the pore in a lateral terminal position (Figure 11B). The diameter of the pore in the *A. loisae* capsules measured 1.9 to 4.0 mm (mean 2.69 mm, n = 4). The lateral borders of these capsules were smooth.

Description of the Juveniles

The fifty intracapsular larvae of *A. fontainei* were in an advanced stage of development.

Their shells were thick, well calcified and fusiform, with lengths ranging from 3.12 to 3.25 mm (Figure 3). The protoconch was rounded with 1.5 whorls and was covered with a thin, almost smooth, periostracum, with few folds (Figure 5). The teleconch had three convex, smooth whorls, with initiation of spiral, wide grooves on the penultimate whorl. The last, largest whorl, had a diameter almost equivalent to the preceding ones, and its surface bore spiral, better developed grooves (Figure 6), similar to adult individuals. The shell aperture was elongated with an average length of about 1.57 mm and width of about 0.77 mm. The border of the shell aperture was smooth and sharp (Figure 9). The aperture was bordered by a still developing, short, wide siphonal canal, showing the beginning of formation of a columnar callus. It was of interest to note that one specimen was found to have a shell penetration (Figure 7) on the last whorl of the teleconch.

The two intracapsular juveniles of *A. loisae* were not obtained alive. Their shells, similar to those of *A. fontainei*, were thick and well calcified, with the teleconch composed of three convex whorls. Maximum lengths of these juveniles were 3.52 and 3.84 mm (Figure 4). The shell aperture was elongated, with a length of 2.02 mm and width of 0.99 mm. The border of the aperture lip was undulated due to the presence of


3
4
5
200 µm
6
7
50 µm
8
20 µm
9
500 µm
10
20 µm

external ribs, in clear contrast to that of *A. fontainei* (Figure 10). The protoconch bore similar characteristics to those of *A. fontainei*, although greater detail was not available due to the eroded condition of the specimens. Table 3 gives the numbers and measurements of egg capsules and juvenile specimens of both species studied.

External Anatomy of Adults (Figures 11C, D)

The study of the external anatomy of *A. fontainei* and *A. loisae* was based on specimens who had been formalin-fixed, and thus the measurements obtained represent partially constricted structures.

From the ventral aspect, both *A. fontainei* and *A. loisae* showed a broad foot which was dark reddish in color, with the lateral border granulose where the propodial groove was observed. The posterior portion of the foot bore a large, horny operculum which was dark brown in color, showing growth rings. The operculum was oval shaped with a pointed tip directed toward the left (Figures 11F, H). In both species the nucleus of the operculum is marginal. The maximum length of the *A. fontainei* operculum was 19.15 mm (n = 2) and that of *A. loisae* 22.4 mm (n = 1). Operculum is of moderate size (2/3 aperture length), ovate and corneous.

In both species the mantle was observed as a broad sheet with a smooth border, and to be unpigmented. Its left anterior region was extended as a semi tubular, elongated siphon. It was noted that the *A. loisae* siphon was thinner and longer than that of *A. fontainei*.

The heads of both *A. fontainei* and *A. loisae* each had two retractile tentacles. The lateral part of the anterior third of each tentacle bore easily visible pigmented eyespots.

The penis of the male specimens was located above the right tentacle and immediately beneath the mantle edge. The penis of *A. fontainei* was 30.8 mm long; it was relatively thick, with its proximal portion widened to 8.6 mm, representing 27.9% of its total length. The distal end of the penis was thin and pointed (Figures 11C, E). The penis of *A. loisae* (Figures 11D, G) was relatively larger, with a length of 32.6 to 37.5 mm (mean 34.7; n = 3). It differed from that of *A. fontainei* in being thicker in proximal and median sections, with the proximal thickness representing 30% of its' total length. Its' tip was blunt and not pointed as observed in *A. fontainei*.

Both species presented a notable vas deferens as a thick cord running along the right side of the mantle floor. The soft parts of the female specimen of *A. fontainei* were anatomically similar to those of the males, except for the presence of the penis and vas deferens.

DISCUSSION

The findings of the present study extend the range of these species to the Chilean fjord region to 45°21'S. Existing literature does not present reproductive or morphological details, which makes the present study of interest as the specimens were found during a reproductive period.

The presence of egg capsules on the shells of *A. fontainei* and *A. loisae* represent specialized behavior typical of species from deep water habitats with soft bottoms. They probably deposit egg capsules on each other's shells when unable to find other hard substrates suitable for receiving the capsules. This type of adaptation has also been observed in *Chorus giganteus* Lesson, 1829, which live on muddy sand bottoms between 8 and 30 m depth. Here, gregarious reproductive behavior of this species culminates in deposition of egg capsules on the shells of congeners (Gallardo, 1980). The results of the present study have shown differences between the egg capsules of *A. fontainei* and *A. loisae*. The capsules of *A. fontainei* had indented lateral borders not observed on capsules of *A. loisae*, with the form and positions of indentations unique to each capsule. Other important differences between the species studied included the erect position of the egg capsule, and terminal location of the pore in *A. loisae*, versus the inclined position and lateral subterminal location of the pore in *A. fontainei*. These differences between species which belong to same genus have been observed by Gulbin (2000) who describes the morphology and structure of the egg capsules, young and adult specimens of three species of *Pyrulofusus* in the north Pacific and subarctic region. Results showed differences in the shape of egg capsules and in spiral

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Figure 3. External anatomy of *A. fontainei* juvenile. 3.52 mm in length.
Figure 4. External anatomy of *A. loisae* juvenile. 3.10 mm in length.
Figure 5. Protoconch of *A. fontainei* juvenile. (SEM).
Figure 6. Grooves on teleconch of *A. fontainei* juvenile. (SEM).
Figure 7. Shell perforation, juvenile *A. fontainei*. (SEM).
Figure 8. Shell perforation from Figure 7, enlarged. (SEM).
Figure 9. Shell aperture, *A. fontainei* juvenile. (SEM).
Figure 10. Shell aperture, *A. loisae* juvenile (SEM).

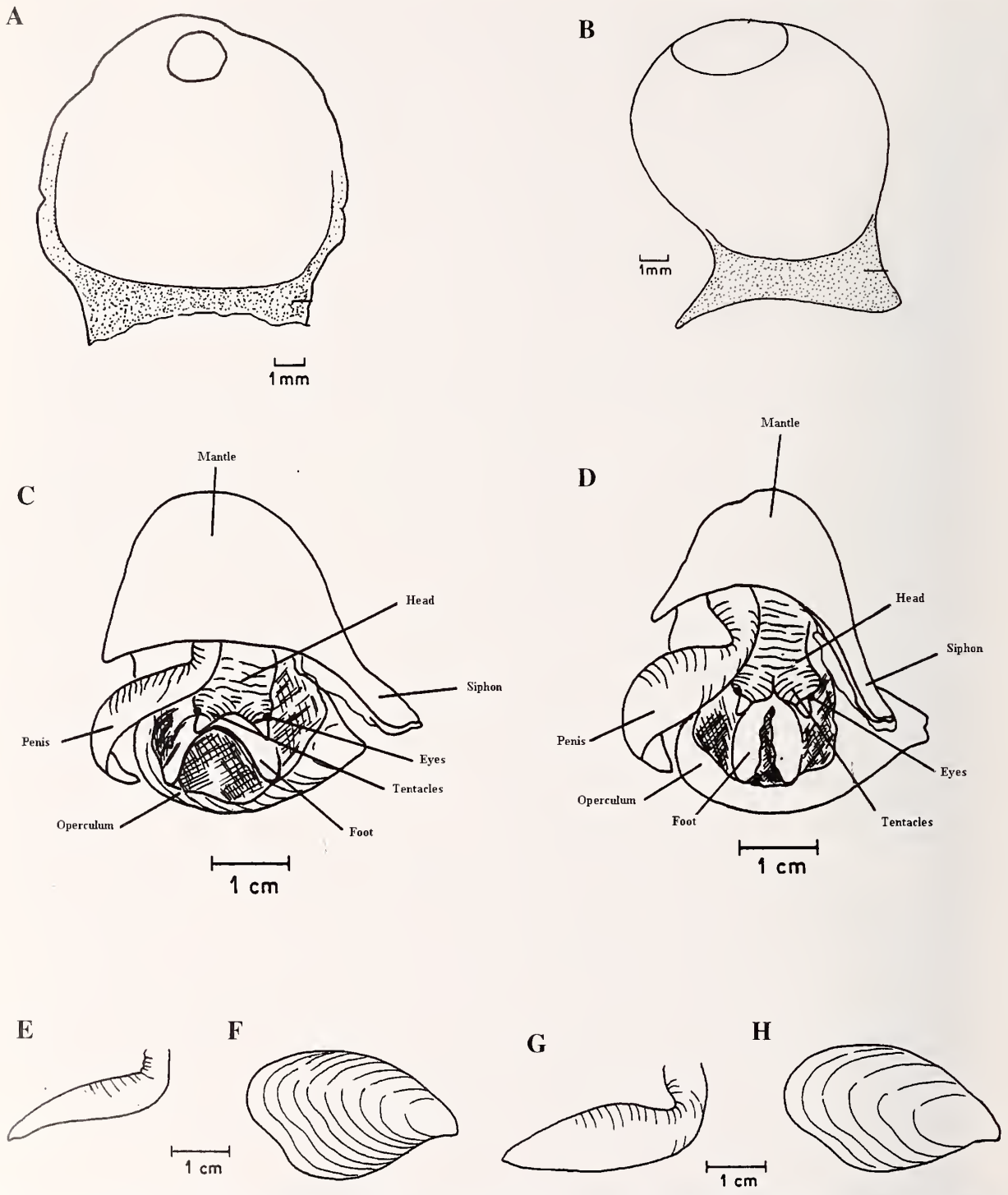

Figure 11. Capsules and external anatomy of adult *A. fontainei* and *A. loisae*. A. Anterior view of an *A. fontainei* egg capsule. B. Anterior view of an *A. loisae* egg capsule. C. Soft parts of *A. fontainei*. D. Soft parts of *A. loisae*. E. Penis of *A. fontainei*. F. Operculum of *A. fontainei*. G. Penis of *A. loisae*. H. Operculum of *A. loisae*.

Table 3

Counts and measurements on egg capsules and juveniles of *A. fontainei* and *A. loisae* obtained during CIMAR Fjord Cruises 7 and 8.

Species	Rows	Egg capsules			Juveniles	
		Number	Large (mm) (mean ± SD)	Width (mm) (mean ± SD)	Number/egg capsule (mean ± SD)	Large (mm) (mean ± SD)
Cruise CIMAR Fjord 7						
A. fontainei	1	9	9.83 ± 0.38	8.76 ± 0.26	6.33 ± 2.08	3.25 ± 0.52
	2	11	9.34 ± 0.33	8.35 ± 0.23	6.20 ± 1.48	3.12 ± 0.28
	3	12	10.04 ± 0.50	9.48 ± 0.27	Rest	—
Cruise CIMAR Fjord 8						
A. loisae	1	7	8.90 ± 0.37	7.90 ± 0.84	2.0*	3.68 ± 0.23

* Observation: Juveniles in *A. loisae* were found in an open and semi-broken egg capsule.

sculpture in young specimens in the three species of this genus.

Also, differences observed in the sizes and stages of development of intracapsular juveniles from the three rows of capsules obtained from the female *A. fontainei* suggested that each row may have been produced by a different female. A similar observation was recorded by Gallardo (1981) for capsule deposition by *Chorus giganteus* observed in the laboratory.

The transparent liquid observed within the capsules of *A. fontainei* in which were suspended the juveniles and tissue remains may have contained remnants of nutritive eggs, suggesting that the juveniles of this species may be adapted to lecithotrophic feeding as also observed by Gallardo (1981) for *Chorus giganteus*; West (1983) for the buccinid *Colus stimpsoni* Mörch, 1867 and Martell et al. (2002) in *Buccinum thermophilum*. This phenomenon is thus a broadly distributed developmental strategy among the neogastropods. However, Gulbin (2000) observed in *Pyrulofusus dexius* (Dall) that there is an additional food source, the protein layer of the capsule.

Shell boring is a broadly recognized predatory strategy among the muricids (Gordillo & Amuchastegui, 1998), both in early stages of development and in adults. Cannibalism among juveniles as young as 10 days in age has been observed in *Chorus giganteus* when other naturally occurring food is unavailable (Gonzalez & Gallardo, 1999). Similar behaviour between encapsulated individuals may explain our observation of shell penetration seen in *A. fontainei* (Figure 7), as well as the apparent radular attack observed on shell borders of other larvae in the capsule (Figure 8).

The form of the penis shows large variation among molluscs, and is the anatomical characteristic of most importance among the Littorinidae (Reid, 1986). Observations on individuals of the presently studied species of *Aeneator* indicate there is no external sexual dimorphism between shells of adult males and females, but sexual dimorphism is notable from the soft parts, when considering the presence of a well developed penis in the males. In this study the two species were readily separated based on the longer and basally thicker penis in the male *A. loisae*, compared with that of *A. fontainei*.

Table 4

Comparison between numbers and size of juveniles and adults of gastropods with direct development.

Species	Number juveniles/capsules	Size juveniles (mm)		Length adults (mm)	Authors
		Range	Mean		
Adelomelon brasiliana	9–33	—	~10.0	160	Nuñez y Narosky (1997)
Zidona dufresnei	2–6	—	18.0	207	Nuñez y Narosky (1997)
Acanthina monodon	10–122	0.83–1.30		65	(Gallardo, 1979)
Trophon geversianus	5–45	—	3.0	82	Gallardo & González (1994)
Trophon plicatus	3–38	1.8–3.3	—	50.0	Penchaszadeh, 1976 Pastorino, 2005
Aeneator fontanei	2–8	3.12–3.25	—	103–128	Present study
Aeneator loisae	2*	3.52–3.84	—	105–128	Present study

* Observation: Juveniles in *A. loisae* were found in an open and semi-broken egg capsule.

The large size of the juveniles (Table 4) produced by species with holobenthic development may be an adaptation to intracapsular development. The additional food source by nurse eggs (Gallardo & Gonzalez, 1994), protein layer capsules (Gulbin, 2000) and intracapsular cannibalism (present work) may enable the individuals to hatch at a large size immediately suited for survival in the adult habitat.

Finally, all species mentioned have in common a high latitude distribution and direct embryonic development. However, species vary in sizes and numbers of their eggs and in the range of juvenile size and/or capsule number, so it is difficult to generalize about species with direct development.

Literature existing prior to the present study classified *A. fontainei* and *A. loisae* strictly on the basis of shell morphology. Our data on reproductive characteristics, such as oviposition, egg capsule structure and larval morphology, and anatomical observations of adult soft parts, now broadens their taxonomic characterization.

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LITERATURE CITED

ALARCON, E., E. ACUÑA, R. CATALAN & J. C. VILLARROEL. 1999. Descripción de parámetros poblacionales en tres especies simpátricas de la III y IV regiones de Chile: *aeneator fontainei*, *A. castillai* y *A. loisae* (Mollusca, Gastropoda, Buccinidae). Summary IV Congreso Latinoamericano de Malacología: 37. Coquimbo, Chile.

D'ORBYGNY, A. 1834–1847. Voyage dans l'Amerique Meridionale 5 (3): Mollusques. P. Bertrand: Paris.

GALLARDO, C. S. 1979. Developmental pattern and adaptations for reproduction in *Nucella crassilabrum* and other muricacean gastropods. Biological Bulletin 157:453–463.

GALLARDO, C. S. 1980. Adaptaciones reproductivas en gastrópodos muricáceos de Chile; conocimiento actual y perspectivas. Investigaciones Marinas 8(1–2):115–128.

GALLARDO, C. S. 1981. Posturas y estadio de eclosión del gastrópodo Muricidae *Chorus giganteus* (Lesson, 1829). Studies on Neotropical Fauna 16:35–44.

GALLARDO, C. S. & K. A. GONZALEZ. 1994. Ovispostura y desarrollo intracapsular de *Xanthochlourus cassidiformis* (Blainville, 1832) (Gastropoda, Muricidae) de la costa sur de Chile. Gayana Zoología 58(1):79–90.

GONZALEZ, K. A. & C. S. GALLARDO. 1999. Embryonic and larval development of the muricid snail *Chorus giganteus* (Lesson, 1829) with an assessment of the developmental nutrition source. Ophelia 51(2):77–92.

GORDILLO, S. & S. AMUCHÁSTEGUI. 1998. Estrategias de depredación del gastrópodo perforador *Trophon geversianus* (Pallas) (Muricoidea: Trophonidae). Malacología 39(1–2):83–91.

GULBIN, V. 2000. The egg capsule and young of the gastropod *Pyrulofusus dexius* (Dall) (Buccinidae: Volutopsiinae). The Veliger 43(2):195–196.

GUZMAN, N., S. SAA & L. ORTLIEB. 1998. Catálogo descriptivo de los moluscos litorales (Gastropoda y Pelecypoda) de la zona de Antofagasta, 23°S (Chile). Estudios Oceanológicos 17:17–86.

HARASEWYCH, M. G. & Y. I. KANTOR. 2002. *Buccinum thermophilum* (Gastropoda: Neogastropoda: Buccinidae), a new species from the endeavour vent field of the Juan de Fuca Ridge. Journal of Molluscan Studies 68:39–44.

HAYASHI, S. 2005. The molecular phylogeny of the Buccinidae (Caenogastropoda: Neogastropoda) as inferred from the complete mitochondrial 16 S rRNA gene sequences of selected representatives. Molluscan Research 25(2):85–98.

KANTOR, Y. 2003. Comparative anatomy of the stomach of Buccinoidea (Neogastropoda). Journal Molluscan Studies 69:203–220.

KEEN, M. 1971. Sea shells of Tropical West America. Marine Mollusks from Baja California to Perú. Stanford University Press. 1063 pp.

MARTELL, M. A., V. TUNNICLIFFE & I. R. MACDONALD. 2002. Biological features of a buccinid whelk (Gatropoda, Neogastropoda) at the endeavor vent fields of Juan de Fuca Ridge, Northeast Pacific. Journal Molluscan Studies 68:45–53.

MCLEAN, J. H. & H. ANDRADE. 1982. Large archibenthal Gastropods of central Chile: collections from an expedition of the R7V Anton Bruun and the Chilean Shrimp fishery. Contribution Science Natural History Museum Los Angeles County 342:1–20.

NUÑEZ, C. & T. NAROSKY. 1997. Cien caracolas argentinas. Editorial Albatros: Argentina. 146 pp.

OSORIO, C., D. REID & L. RAMAJO. 2005. Moluscos en los canales del sur de Chile entre Boca del Guafo y Estero Elefantes (Cimar 7 Fiordos). Ciencia y Tecnología del Mar 28(1):91–98.

OSORIO, C., R. PEÑA, L. RAMAJO & N. GARCELON. 2006. Malacofauna bentónica en los canales oceánicos del sur de Chile (43°–45°S). Ciencia y Tecnología del Mar 29(1): 103–114.

PASTORINO, G. 2005. A revision of the genus *Trophon* Montfort, 1810 (Gastropoda: Muricidae) from southern South America. The Nautilus 119(2):55–82.

PENCHASZADEH, P. E. 1976. Reproducción de gasterópodos prosobranquios del Atlántico Suroccidental. El género *Trophon*. Physis A 35(90):69–76.

RAMIREZ, B. J. 1990. Moluscos de Chile. 3° Neogastrópoda. Not Published: Santiago, Chile.

REID, D. G. 1986. The littorinid molluscs of mangrove forests in the Indo-Pacific region. British Museum (Natural History): London. 227 pp.

VAUGHT, K. C. 1989. A classification of the living Mollusca. American Malacologists, Inc.: USA. 189 pp.

WEST, D. L. 1983. Reproductive biology of *Colus stimpsoni* (Prosobranchia: Buccinidae) V. Nutritive egg formation. The Veliger 25(4):299–306.